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Establishing climatic constraints shaping the distribution of alien plant species along the elevation gradient in the Alps

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Abstract

In this work, we analyse the role of climatic constraints in shaping the distribution of alien plant species along the elevation gradient in the European Alps. Alien species occurrence was recorded in 278 plots located beside rivers, from 100 to 2,100 m a.s.l. Climate variables were calculated from the data recorded by 145 meteorological stations and interpolated by a multiple regression approach. Both richness and occurrence of aliens were modelled. In particular, relationships between the occurrence of alien plants and (1) elevation or (2) the climatic variables, were tested by applying generalised linear models and generalised linear mixed models; the model parameters obtained were used to estimate upper elevation limits of alien occurrence and their related climate values. Sixty-eight alien species were encountered, the majority (71%) invasive in Italy and worldwide. A steep decrease in alien species richness with elevation was found, with the probability of alien species occurrence decreasing by half for each 100 m increase in elevation. Minimal adequate models based on (1) non-transformed climatic variables and (2) derived PCA values, confirmed that occurrence of alien plant species along the elevation gradient was positively related to the minimum temperature, the mean temperature and the heat sum for the spring season, rather than to the incidence of absolute minimum temperature and frost days, as usually assumed. Although further experimental analyses are needed, these results support the hypothesis that, referring to climate factors, elevation limits along rivers are mainly established by low spring temperatures which operate at the level of population viability rather than plant survival.

Introduction

Mountain regions, widely recognized as important biodiversity hot spots with rich, distinct floras, are increasingly threatened by invasive alien plants as a consequence of human impact (Bear et al. *2006*). The interest of ecologists in the biological invasion of mountain systems has recently increased with the aim of gaining further insight on patterns of invasion and the mechanisms driving them along the elevation gradient (Alexander et al. *2011*).

On temperate mountains, a continuous decrease in alien plant species richness with elevation has been noted (Becker et al. *2005*; Mallen-Cooper and Pickering *2008*; Pauchard and Alaback *2004*) with areas above the timberline little affected by aliens. This trend was explained in terms of four major factors which change with increasing elevation (Pauchard et al. *2009*): (i) abiotic natural factors (topography, soil and climate) which become harsher; (ii) decreasing disturbance; (iii) reduced propagule supply; and (iv) higher resistance of native plant communities. Thus, once elevation has been chosen as a predictor of invasive species richness, it has to be considered as a proxy of many implicit factors that could, separately or in combination, limit the spread of alien plants.

Relationships between climate and biological invasions have been widely investigated to predict potential distribution of alien plants using a climate matching approach (Broennimann et al. *2007*; Richardson and Thuiller *2007*). Some criticisms have been made of correlative approaches by pointing out that (i) the observed species distributions may be constrained by non-climatic processes (Guisan and Zimmermann*2000*; Pearson and Dawson *2003*) such as disturbance, biotic interactions and limited propagule dispersal, (ii) the present limits may not be in equilibrium with the environment because the range may still be expanding (Collingham et al. *2000*) and (iii)

correlative approaches do not reveal the mechanisms by which climate drives plant distribution (Williamson *2006*).

Despite these limitations, species distribution models based on statistical relationships between occurrence data and underlying climatic conditions are increasingly used to describe or predict spatial patterns of biological invasions (Thuiller et al. *2005*): their results can generate rigorous hypotheses about the causes of the distribution patterns observed, and provide useful knowledge to steer preventive and control measures. Moreover, it is extremely important to identify climatic constraints affecting the spread of alien species in the general global-warming scenario (Bear et al. *2006*; Walther et al. *2009*).

Most studies on biological invasion of mountain systems, only rely on climate as a potential factor constraining alien plant distribution, but few statistical correlations have been undertaken to assess if climate actually plays the dominant role (Marini et al. *2009*, Marini et al. *2011*), and which climatic predictors are most important.

Invasion in the Alps mainly occurs in two human-influenced habitats, road verges and riversides, which stretch along valleys acting as corridors for alien species spread. Road verges, chosen as study sites in some previous work (Becker et al. *2005*; Pickering and Hill *2007*; Alexander et al. *2009a*) display differences in management (e.g. mowing), in aspects and neighbouring vegetation communities. On the contrary, riparian zones are more uniformly affected by natural and anthropogenic disturbances along the whole elevation range considered. This favours both dispersal and establishment of alien plant species, for instance on bare surfaces and in unsaturated systems, where competition with native species is low.

In this paper, we analyse the role of climatic constraints in shaping the distribution of alien plant species along an elevation gradient beside rivers located in the Italian Alps, with main focus on the upper elevation limits.

Methods

Study area

The study was conducted in Piedmont (Fig. 1), the Italian region lying in the southern foothills of the Western Alps between 44°02′–46°26′N and 06°49′–08°32′E. The area, although small, is characterized by different topographies: the Western part of the alluvial Po plain, surrounded by high mountains on the border with France and Switzerland. The steep gradient (from 100 m to 4,000 m a.s.l.) across less than 100 km, strongly influences the climate which shows wide variation in temperature and precipitation over short distances.

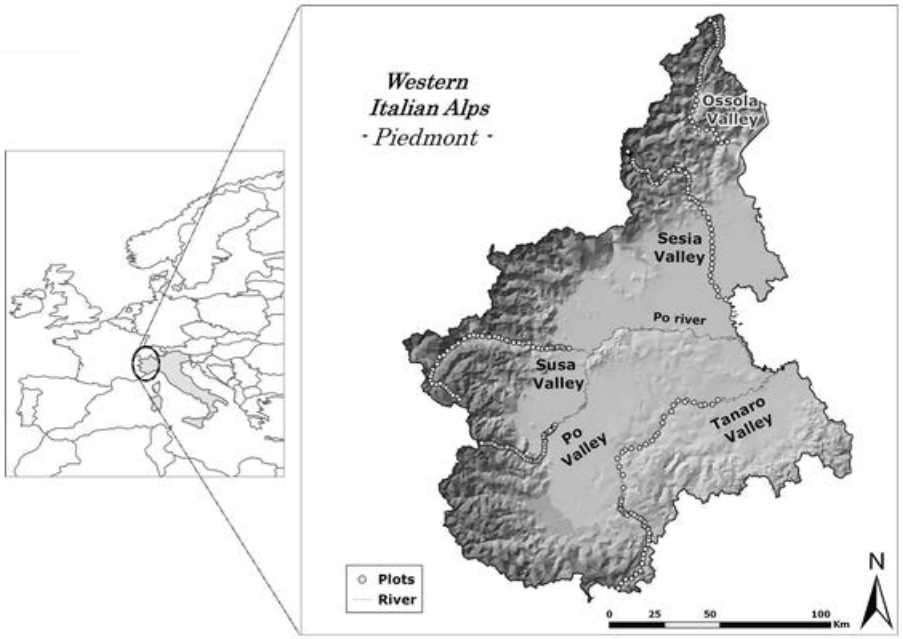


Fig. 1
Study area

Mean annual temperature varies with elevation, from 11–12°C in the plain to 1°C for areas at about 2,400 m. Mean annual rainfall ranges from 500–700 mm in the plain and in western inner alpine valleys to 2,000 mm and above in the northern pre-alpine and alpine areas. There is a pronounced maximum in spring, and a minor peak in autumn, with the minimum usually in winter.

The Po plain is characterized by heavy human impact that favoured the introduction and spread of many alien plants (Celesti-Grapow et al. *2010*). The lowland is connected to the mountains by rivers and roads. Humans have used the mountainous region intensively for the last three centuries, so we suppose that at least the most invasive species had time and opportunity to get established in favourable sites, reaching their physiologically determined elevation limits (Pyšek et al. *2011*). In the last few decades, rivers appeared more and more affected by several forms of human disturbance even at high elevations, e.g. stream channelization, which imply soil displacement by heavy machinery from downstream to upstream. Furthermore, the expansion of tourism in villages historically located along streams led to an increase in utilization and eutrophication. Information on native vegetation types are reported in Siniscalco et al. (*2011*).

Sampling design and data collection

Data were collected at the plot scale. Plots were selected following a systematic sampling design (Elzinga et al. *2001*) along five alpine valleys (Ossola, Susa, Po, Sesia and Tanaro). Along each valley, a series of 3 × 7 m plots, regularly spaced 1.5 km apart, were placed in the riparian zone. Since many alien plants are early seral species that thrive in the low-competition environments created by frequent disturbance, lateral limits for the sampling area were the approximate maximum annual wetted width of the river corridor.

The number of plots per valley ranged from 44 to 72 according to the length of the river segments running along the elevation range considered (100–2,100 m). In total, 278 plots were sampled. Within each plot, both alien and native plant species were recorded.

Environmental variables

Raw climate data (daily temperature, precipitation values), recorded by 145 automatic stations (ARPA Piemonte) were used to characterize the climate of each valley. The series used are restricted to the period of automatic registration (from 2001 on) which ensures the most complete and accurate set of data.

Several climate parameters were calculated (complete list in Online Resource 1): mean and absolute temperatures, number of frost days (T min ≤0°C), temperature range, heat sum (threshold temperature 4°C), mean rainfall. Climate variables are given as annual and seasonal means. Topographic features (elevation, aspect, slope and distance from the valley bottom) were derived from the Digital Elevation Model for each station and used along with latitude and longitude as independent variables to interpolate climate surfaces.

Using digital layers for each independent variable and applying basic GIS techniques, as proposed by Ninyerola et al. (*2000*), the multiple regression equations were used to obtain all the climate variable values, as influenced by geographic and topographic features, for each of the 278 vegetation plots.

Alien species distribution models

The effects of elevation and of the selected climatic factors on alien species occurrence were tested by a modelling approach. A preliminary non parametric Wilcoxon pair-wise test was carried out to highlight the differences in the elevation pattern of alien species richness (number of alien species per plot) among the valleys. The test was then performed on the whole data set (five valleys together), to analyse the pattern of alien species richness with respect to six elevation classes (range of 300 vertical metres each).

Existing relationships between the occurrence of alien plants and (1) elevation or (2) all the available climatic parameters, were tested by applying Generalised Linear Models (GLM—McCullagh and Nelder *1989*) and Generalised Linear Mixed Models (GLMM, Bolker et al. *2009*). The response variable was represented by a binary variable for both GLM and GLMM models (presence/absence of alien species). We decided to apply GLMM, considering that the study sites were nested within the five Alpine valleys: in this way we could check for non independence in the presence-absence values given by the grouping factor Valley. In GLMM, the factor valley was included as a normally distributed random effect intercept to account for spatial correlation. For both the approaches, the response variables were tested against the linear and the second order polynomial fit of each predictor. The transformation that contributed most in reducing the variance of the response was statistically determined by a Chi-squared test (linear vs. polynomial fit) and the optimal transformation was then included in the model. Following this procedure, the most explicative climatic variable within each group was selected and included in the full model (this procedure was adopted to reduce multicollinearity due to the interpolating process adopted to calculate climatic variables). Backward and forward stepwise variable selection procedures based on the Akaike Information Criterion (AIC, Hastie and Pregibon *1992*), were then applied to estimate the minimal adequate model, defined as the model explaining the highest proportion of variation using the smallest number of variables. The final reduced model was obtained when both methods converged to the same result. For this reduced model, a measure of 'goodness of fit', the adjusted D^2 (D_{adj}^2) was calculated (the D_{adj}^2 ranges from 0—no fit to 1—perfect fit; Guisan and Zimmermann *2000*) and, to avoid the occurrence of multicollinearity in the predictors retained in the minimal model, the Variance Inflation Factor (VIF, Fox and Monette *1992*) was computed.

A leave-one-out (LOO) cross-validation estimate of prediction error (Davison and Hinkley *1997*) was also calculated.

Both GLM and GLMM were applied also on derived PCA values. In order to reduce subjectivity in the selection of climatic parameters to be introduced into the full model, variables related to temperature were summarized by principal component analysis (PCA) and coordinates of the new PCA axes used as new climatic parameters (Ohlemüller et al. *2006*).

All models were built using the R software and the glm and glmer functions (R Development Core Team*2011*).

Results

Data summary

The pooled data set from the five valleys contained 68 alien species, most were invasive in Italy and worldwide (71%), 25% were naturalized and 4% casual species (status assigned following Celesti-Grapow et al. *2009*). Herbaceous annuals were dominant (56%), while perennials accounted for 28% and woody species for 16%. Analyses on status, residence time, origin and traits of the alien *taxa* are reported in Siniscalco et al. (*2011*).

The elevation pattern of alien species richness, explored between valleys by the Wilcoxon pair-wise test, revealed a general consistency in the shape of the relationship (Table 1; Fig. 2).

Table 1

Results of the non-parametric Wilcoxon pair-wise test performed for the number of alien species between the five valleys sampled. *p* values were displayed (the Holm correction for *p* value was used)

Valley	Po	Sesia	Susa	Tanaro	Ossola
Po	1				
Sesia	1	1			
Susa	0.380	0.103	1		
Tanaro	0.272	0.448	**0.003**	1	
Ossola	1	0.940	0.800	0.118	1

In *bold*, significant values are highlighted

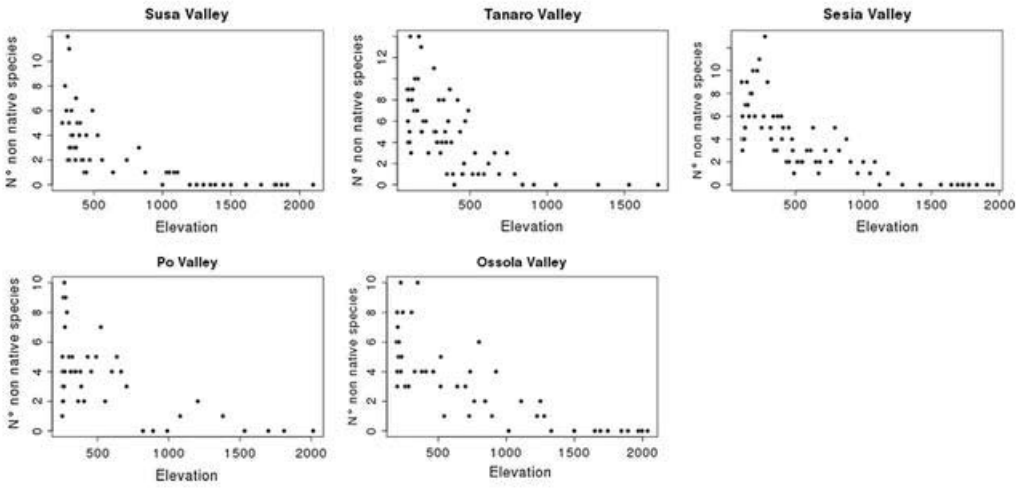


Fig. 2

Relationship between the number of alien species per plot and elevation in each valley sampled

The number of aliens was highest in the first elevation class (Fig. 3), up to 428 m, with strong differences among plots, ranging from 0 to 14. A consistent reduction occurred between classes up to the 1,100–1,430 m class, where the number of aliens drops off towards zero. All classes (excluding the last two, where alien species were absent) differed strongly from each other.

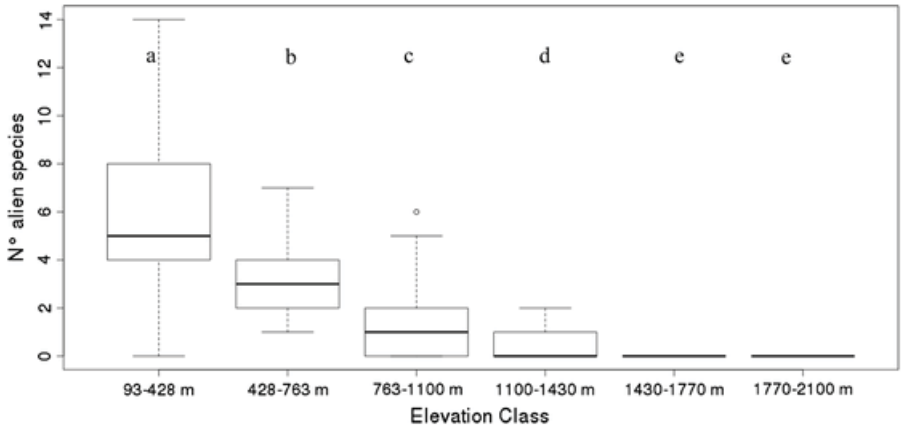


Fig. 3

Boxplot distribution of the alien species number in the selected elevation classes. *Letters* represent significant different distributions ($p < 0.001$) according to the pairwise Wilcoxon test, with Holm adjustment for p values

Occurrence of alien plant species in relation to elevation

Alien plant occurrence resulted highly related to the elevation gradient. Elevation, considered as the only predictor included in this first logistic regressive model, explained about 72% of the total variation and the model presented a good fit (Table 2a).

Table 2

Model summary for the logistic regression model between alien species occurrence and elevation

a

GLM Model parameters	Coefficient	$p(X^2)$	SE	Explained Variance (D_{adj}^2)
Intercept	7.652		1.075	0.720
Elevation	-0.007	<0.001	0.001	

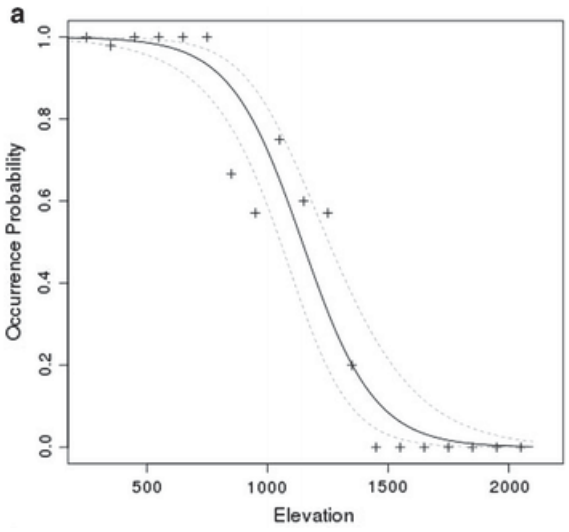
b

GLMM Model parameters	Estimated coefficient	*p* value	SE
Intercept	7.653	<0.001	1.075
Elevation	-0.007	<0.001	0.001

Two models were estimated (a) by classical generalised linear models and (b) by generalised linear mixed models (GLMM) with valley as a grouping factor to account for spatial correlation (estimated standard deviation of random effect for valley = 0.218)

Interpreted as odds ratio, the negative coefficient for elevation suggested that the decrease of alien plant species occurrence for an increase in 100 m altitude is approximately equal to $e^{100*-0.007} = 0.496$ (in a similar way, the confidence intervals at the 1-α level—95% in this case—can be calculated as $e^{100*-0.007 \pm 1.96*100*0.001} = 0.640; 0.408$). That is, on average, the ratio occurrence/non-occurrence is decreased by half for an increase of 100 m in elevation.

Assuming this general model, occurrence probability for alien plants is less than 10% above an altitude of 1,475 m (lower 95% CI 0.03; upper 95% CI 0.23) less than 5% above 1,578 m (lower 95% CI 0.01; upper 95% CI 0.15) and less than 1% above 1,834 m (lower 95% CI >0.001; upper 95% CI 0.009, Fig. 4 a, b).



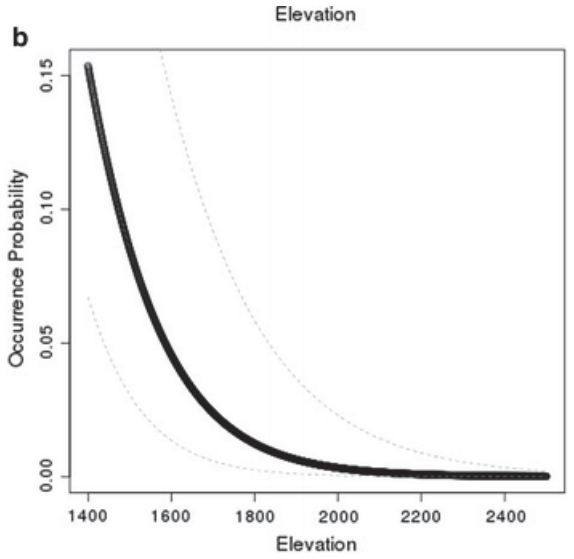


Fig. 4

Plots of the estimated logit function for the predictive model explaining alien species occurrence with respect to elevation gradient. (**a**) Presence/absence of alien species in each sampled area plotted against elevation; *black crosses* represent the mean occurrence values calculated within 100 m wide elevation classes; *dotted lines* represent the estimated confidence intervals (95%) for the logit function. (**b**) Detail of the probability function estimated for alien plant species occurrence with respect to the elevation range between 1,400–2,500 m. *Dotted lines* represent 95% CI

Interestingly, for the performed GLMM model (Table 2b), estimated coefficients had exactly the same values and the same negative sign with respect to the GLM model (Table 2a), confirming the general decay of alien plant species at high elevations and the generality of this result, irrespective of the considered valley.

Alien species occurrence in relation to climatic factors

Deviance reduction was calculated for each climatic predictor of the occurrence of alien species (Online Resource 2). Both linear and second-order polynomial fits were calculated by iterative procedures and tested for the best fit. High variability in deviance reduction was observed among and within each group of climatic variables. In general, the climatic variables describing warmer temperatures and thermal requirements of plants (i.e. maximum temperatures, heat sums) were more related to alien occurrence with respect to parameters expressing cold climatic conditions (i.e. minimum absolute temperatures or number of frost days).

In the same way, comparing seasonal predictors within each group of climatic variables, spring predictors showed the highest degree of explicative power, while the winter predictors were always less effective.

Notably, deviance reduction obtained by PCA axes was very high and comparable with original climatic predictors, confirming the high degree of multicollinearity occurring within climate variable groups.

Based on these data (non-transformed climatic parameters and derived PCA values), both GLM and GLMM were calculated for alien plant occurrence. The GLMMs were not shown since they pointed out the same results of GLMs. In both GLM models, elevation was not included as a

predictor considering its high correlation with the climatic parameters and the suitability to use these more proximal variables to understand the ecological implications of the resulting models.

In the first model, within each group of variables related to temperatures, the predictor with the highest explicative power was selected and included in the model (i.e. for the 'mean temperature' group the mean temperature related to the season 'spring' was selected). Altogether, 11 variables were used. After stepwise selection, only three highly significant predictors were retained into the parsimonious model: minimum spring temperature, temperature range during summer and minimum absolute spring temperature, all three predictors positively correlated with alien plant occurrence (Table 3). The explicative power (deviance reduction) for the minimum spring temperature was about eleven times higher than the deviance reduction obtained for the other two predictors. Moreover, it should be noted that the selected three predictors represented only one of the possible subsets of predictors out of all the combinations of climatic variables initially included in the full model, but, on the other side, this subset could be addressed as the best parsimonious one (maximising the amount of explained variance with the lowest number of predictors), with a high ecological meaning as well.

Table 3 Summary of the minimal model (after stepwise variable selection) for the occurrence of alien species in relation to climate

Response Variable	Mean	Min–Max	No plot	No of variables involved in the Full GLM	Model features			
Alien plant species occurrence	–	0–1	278	11	Binomial distribution, 'logit' link function			
	Variables retained in the minimal GLM							
ID Var.	Deviance reduction	Coefficient value	VIF	$p(X^2)$	Mean Error (LOO cross validation)	D^2_{adj}	r	Difference between Full and Minimal GLM $p(X^2)$
*T*_min_spring	179.53	0.630	5.154	<0.001	0.041	0.765	0.876	0.558
*T*_range_summer	16.05	0.995	1.273	<0.001				
*T*_ab_min_spring	7.66	0.392	6.578	0.047				

Eleven predictors were initially included in the full model: latitude and longitude (both as polynomial terms), Frost_days_spring, Rainfall_winter (as a polynomial term), *T*_max_spring, *T*_mean_spring, *T*_min_spring, Tab_min_spring, Tab_max_spring, Sum_T4_spring, Term_range_summer (as a polynomial term)

The total explained variance was about 76% and no statistical difference existed between the full model and the minimal model (χ^2 test, $p = 0.558$). The included predictors were not correlated among each other (VIF <10) and the mean cross-validated error between predicted and observed alien plant occurrence value was quite low (0.041).

Considering the high resemblance in results, the second model based on derived PCA axes was illustrated in Online Resource 3.

Considering climatic models developed here, we can estimate the relationship between alien plant occurrence and the most explicative predictor, e.g. minimum spring temperature. This relationship showed a probability of alien occurrence lower than 10% when the minimum spring temperature threshold of 0.1°C was exceeded (at an elevation of 1,475 m), a probability lower than 5% when

−0.5°C was exceeded (1,578 m) and a probability lower than 1% when −1.9°C was exceeded (1,834 m).

Discussion

General pattern of alien plants along the elevation gradient

A steep decrease in alien species richness with elevation was found in all the valley examined. This is in agreement with results of previous work on temperate mountain systems (Becker et al. *2005*; McDougall et al. *2005*; Pauchard and Alaback *2004*). Similarity among mountain systems was expected, but the observed similarity in species richness distribution between the valleys analysed was astonishing, considering their differences in ecology, lithology and topography. At the same time, if propagule pressure was the major driver of invasion along valleys, alien plant occurrence at different elevations should be determined by stochastic, dispersal-related processes. Thus, different patterns and elevation limits among valleys would be expected. On the contrary, the resulting similarity among valleys suggests that (i) these species have already reached their maximum potential elevation and (ii) the most effective factors controlling the alien species distribution are those which occur with similar gradients in all the valleys, such as climate (e.g. temperature), overriding the effects of the other factors which are more variable at the local scale. Recent studies (e.g. Alexander et al. *2009a*) found that some invasive forbs showed similar distribution patterns and maximum elevations in both the introduced and native ranges suggesting likewise that temperature, the only factor which varies similarly with elevation in both regions, was an important driver.

Alien species richness was high at lower elevation (up to 428 m) with considerable variation among plots, from sites lacking in aliens to sites bearing up to 14. This is very impressive considering the small plot size and is probably due to the combination of different microhabitats occurring at the plot scale. Moreover, the non-limiting conditions of lowland riparian habitats could promote alien species diversity (Magee et al. *2008*). Moving upwards, alien species number per plot decreased, while their occurrence among plots of the same elevation class was more evenly distributed. Few alien species then, invasive in Italy and worldwide, occurred at intermediate elevation. This fact denotes both suitability of habitats to invasion and propagule dispersal, and at the same time, a rapid response of these species to abiotic constraint changes along the elevation gradient through phenotypic plasticity and/or genotypic differentiation (see Alexander et al. *2009a*and references therein). Plastic responses to environmental variation or local adaptation of advancing populations which originate from low altitude genotypes seem to be more frequent mechanisms of invasion into mountain areas than the direct introduction of genotypes pre-adapted to medium and high elevation (Haider et al. *2010*; Alexander et al. *2011*; McDougall et al. *2011*; Pyšek et al. *2011*).

Taking native species into account, a relatively high richness was found along the whole elevation gradients, showing a weak relationship with elevation and alien plant richness. Furthermore, the high variability among plots within each elevation class suggests that, differently from alien plants, the pattern of native plant richness along rivers responds to the spatial heterogeneity produced by hydrological disturbance rather than to the temperature gradient. Therefore, while a rich pool of native species is maintained also in the two highest elevation classes (above 1,430 m), the absence of alien species reflects the current lack in our alien flora of species pre-adapted to the high elevation climate.

Alien species occurrence in relation to climatic factors

The minimal adequate model confirmed that the distribution of alien plant species along rivers in the alpine valleys studied was determined to a great extent by climate. Three climate factors were the main correlates of alien species occurrence, explaining the largest amount of variation (76%), while the effects of human pressure, edaphic and biotic factors or other climatic variables were less important, and corresponded to the residual variation left to explain.

The importance of climatic variables for alien species distribution and richness with respect to other potential predictors has been reported in other studies. For instance, Ohlemüller et al. (*2006*) found that area and shape of indigenous forest fragments and climatic variables (i.e. mean annual temperature and radiation) explained about 50% of the variation in alien species richness. Similarly, Marini et al. (*2009*) found that the distribution of alien plant species in the eastern Alps was mainly determined by mean annual temperature and, to a lesser extent, by human population density. On the other hand, Marini et al. (*2011*) concluded that the absence of a life form-dependent response to temperature in aliens along the elevation gradient suggests that their distribution is more related to propagule pressure and human disturbance than climate. Therefore, the subject is currently under debate and the publication of data to be shared, seems an urgent need.

Despite the convenience of using a generalized temperature index to analyse plant distributions, we should note that mean temperature does not occur in nature and therefore it should be considered only as an indicator and not as a causal factor (Crawford and Jeffree *2007*). The inclusion in our models of indexes more detailed and directly related to plant physiological processes, such as seasonal variations in temperature, resulted in a sub-set of temperature variables with a stronger explicative power than mean annual temperature alone.

In our study, the most explicative climate variables, among those retained in the two models (i.e. GLM using non-transformed and PCA data), were the minimum temperature, the mean temperature and the heat sum for the spring season (Table A1, A2 in Online Resource 3), showing a positive relationship with the alien plant occurrence along the elevation gradient. Therefore, we can assume that alien plant distribution is mainly influenced by the decrease in spring temperature and the delayed start of the vegetative season, rather than to the incidence of low winter temperature and frost days, which are usually assumed to be the most limiting climate factors in the global distribution of species and thought to cause the upper elevation and northern range limits of many plant species (Larcher *2005*).

The mechanisms underlying patterns and limits of alien species seem to be related to temperature which occurs in the pre-emergence period and during the growing season, regulating processes of emergence and establishment of seedlings, growth and reproduction. On the contrary, climate which occurs outside the vegetative period, mainly linked to physiological mechanisms of resistance and survival to climate extremes seems less important. This result may be related to the fact that most of the alien species found in our study were herbaceous species, while woody plants accounted for a relatively small proportion of the pool and were largely confined to lower elevations. In general, extreme minimum temperatures are recognized as an important climate factor constraining woody perennial plants, while herbaceous plants, respond rather to other climate constraints, such as length of growing season (Woodward *1988*). Ecological filtering due to the climate variables identified in our models may be assumed as one of the potential factors explaining the predominance of herbaceous annual species which was highlighted as one of the main features of alien floras in mountain regions worldwide (McDougall et al. *2011*).

A minimum spring temperature range between 0.1°C and −1.9°C corresponds in our model to the elevation range 1,475–1,834 m, where the probability of alien plant occurrence decreases from 10 to 1%. Most alien plants which have spread in the Alps so far cannot establish durable populations in sites where minimum temperature during pre-emergence (spring) is near zero or lower.

These environmental conditions may act through different mechanisms affecting different stages in the life cycle of alien plants. Cooler spring minimum temperature may correspond to an increase in frequency of spring frost events which kill seedlings. The persistence of snow cover in spring could be a key factor for aliens requiring relatively high temperatures or temperature sums to start their development (Ross et al.*2008*). The decrease of accumulated temperature in spring, in the pre-emergence period at mid and high elevations, induces plants to germinate or sprout later and consequently to complete growth and reproduction in a shorter time (Griffith and Watson *2005*). We expect then a selection along the elevation/climatic gradient favouring those species able to adapt particular life-history traits, e.g. growth rate during the juvenile phase, flowering time and trade-off between resource allocation to vegetative growth or reproduction. These adaptive strategies cope with the reduced time and resources, allowing alien species to complete reproduction before the end of the season, as do native herbaceous species (Hautier et al. *2009*).

Observations of clinal patterns of growth and reproductive traits along the elevation gradient seem to confirm these hypotheses (Alexander et al. *2009b*; Baret et al. *2004*; Monty and Mahy *2009*) for some invasive species, highlighting a reduction in plant size, growth rate and number of flowers as adaptations to shorter growing seasons. Willis & Hulme (*2002*) showed that plants of *Impatiens glandulifera*, a alien species frequently found in our study at medium/high elevation were smaller and produced fewer seeds with increasing elevation and that maximum height and fruit production were correlated with increasing post-emergence heat sum. The phenological delay at higher elevations induces *Erigeron annuus* to change its life-history traits from winter annual to biennial, postponing seed germination from the autumn to the spring, when seedlings have a full growing season to reach a sufficient rosette size before the next winter (Trtikova et al. *2010*).

Since scattered individuals of invasive plants may occur beyond the maximum elevation limits reached by their stable populations (Poll et al. *2009*; Ross et al. *2008*), it is possible to assume that elevation limits are established by climatic constraints which operate at the level of population viability rather than plant survival. Such results may be crucial for generating hypotheses and research questions to guide further experimental research.

Referring to climatic factors, alien plant invasion in high mountain areas seems to be mainly constrained by cold springs and short growing seasons. Nevertheless, rising concern is reported (Pickering et al. *2008*) about the upward spread of aliens as a consequence of climate warming and increasing human pressure in mountain systems. Increases in minimum temperature during recent decades in the Alps have been documented (Beniston et al. *1997*) and a significant upward shift in species optimum elevation has been reported, in particular for species having faster population turnover (Lenoir et al. *2008*). The rise in elevation limits of alien plant populations should be monitored carefully, although it is a slow process. Distribution models can help to quantify the current extent of invasion, to predict potential distribution, and target locations for early detection and invasion control. Monitoring existing populations is important but preventing the introduction of pre-adapted species is the more urgent goal (McDougall et al. *2011*), giving special attention to herbaceous species which can flower over a short time period and later in the season.

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References

Alexander JM, Edwards PJ, Poll M, Parks CG, Dietz H (2009a) Establishment of parallel altitudinal clines in traits of native and introduced forbs. Ecology 90:612–622

Alexander JM, Naylor B, Poll M, Edwards PJ, Dietz H (2009b) Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. Ecography 32:334–344

Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, MIREN Consortium (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. PNAS 108:656–661

Baret S, Maurice S, Le Bourgeois T, Strasberg D (2004) Altitudinal variation in fertility and vegetative growth in the invasive plant *Rubus alceifolius*Poiret (Rosaceae), on Réunion island. Plant Ecol 172:265–273

Bear R, Hill W, Pickering CM (2006) Distribution and diversity of exotic plant species in montane to alpine areas of Kosciuszko National Park. Cunninghamia 9:559–570

Becker T, Dietz H, Billeter R, Buschmann H, Edwards PJ (2005) Altitudinal distribution of alien plant species in the Swiss Alps. Perspect Plant Ecol Evol Syst 7:173–183

Beniston M, Diaz HF, Bradley RS (1997) Climate change at high elevation sites: an overview. Clim Chang 36:233–251

Bolker MB, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. TREE 24:127–135

Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701–709

Celesti-Grapow L, Alessandrini A, Arrigoni PV, Banfi E, Bovio M, Brundu G et al (2009) The inventory of the alien flora of Italy. Plant Biosyst 143:386–430

Celesti-Grapow L, Alessandrini A, Arrigoni PV, Assini S, Banfi E, Barni E et al (2010) Alien flora of Italy: species distribution and threats. Plant Biosyst 144:12–28

Collingham YC, Wadsworth RA, Huntley B, Hulme PE (2000) Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. J Appl Ecol 37:13–27

Crawford RM, Jeffree CE (2007) Northern climates and woody plant distribution. In: Børre Ørbæk J, Kallenborn R, Tombre I, Hegseth EN, Falk-Petersen S, Hoel AH (eds) Arctic alpine ecosystems and people in a changing environment. Springer, Berlin, pp 85–104

Davison AC, Hinkley DV (1997) Bootstrap methods and their application. Cambridge University Press, Cambridge

Elzinga CL, Salzer DW, Willoughby JW, Gibbs JP (2001) Monitoring plant and animal populations. Blackwell Science, Malden

Fox J, Monette G (1992) Generalized collinearity diagnostics. J Am Stat Assoc 87:178–183

Griffith TM, Watson MA (2005) Stress avoidance in a common annual: reproductive timing is important for local adaptation and geographic distribution. J Evol Biol 18:1601–1612

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Haider S, Alexander J, Dietz H, Trepl L, Edwards PJ, Kueffer C (2010) The role of bioclimatic origin, residence time and habitat context in shaping alien plant distributions along an altitudinal gradient. Biol Invasions 12:4003–4018

Hastie TJ, Pregibon D (1992) Generalized linear models. In: Chambers JM, Hastie TJ (eds) Statistical models. S.Wadsworth & Brooks/Cole, Pacific Grove

Hautier Y, Randin CF, Stöcklin J, Guisan A (2009) Changes in reproductive investment with altitude in an alpine plant. J Plant Ecol 2:125–134

Larcher W (2005) Climatic constraints drive the evolution of low temperature resistance in woody plants. J Agric Meteorol 61:189–202

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771

Magee TK, Ringold PL, Bollman MA (2008) Alien species importance in native vegetation along wadeable streams, John Day River basin, Oregon, USA. Plant Ecol 195:287–307

Mallen-Cooper J, Pickering CM (2008) Linear declines in exotic and native plant species richness along an increasing altitudinal gradient in the Snowy Mountains, Australia. Austral Ecol 33:684–690

Marini L, Gaston KJ, Prosser F, Hulme P (2009) Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. Glob Ecol Biogeogr 18:652–661

Marini L, Battisti A, Bona E, Federici G, Martini F, Pautasso M, Hulme PE (2011) Alien and native plant life-forms respond differently to human and climate pressures.

McCullagh P, Nelder JA (1989) Generalized Linear Models. Chapman & Hall, London

McDougall KL, Morgan JW, Walsh NG, Williams RJ (2005) Plant invasions in treeless vegetation of the Australian Alps. Perspect Plant Ecol Evol Syst 7:159–171

McDougall KL, Alexander JM, Haider S, Pauchard A, Walsh NG, Kueffer C (2011) Alien flora of mountains: global comparisons for the development of local preventive measure against plant invasions. Divers Distrib 17:103–111

Monty A, Mahy G (2009) Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. Oecologia 159:305–315

Ninyerola M, Pons X, Roure JM (2000) A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. Int J Climatol 20:1823–1841

Ohlemüller R, Walker S, Wilson JB (2006) Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species. Oikos 112:493–501

Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. Conserv Biol 18:238–248

Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ et al (2009) Ain't no mountain high enough: plant invasions reaching new elevations. Front Ecol Environ 7:479–486

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371

Pickering C, Hill W (2007) Roadside weeds of the Snowy Mountains, Australia. Mt Res Dev 27:359–367

Pickering CM, Hill W, Green K (2008) Vascular plant diversity and climate change in the alpine zone of the Snowy Mountains, Australia. Biodivers Conserv 17:1627–1644

Poll M, Naylor BJ, Alexander JM, Edwards PJ, Dietz H (2009) Seedling establishment of Asteraceae forbs along altitudinal gradients: a comparison of transplant experiments in the native and introduced ranges. Divers Distrib 15:254–265

Pyšek P, Jarošík V, Pergl J, Wild J (2011) Colonization of high altitudes by alien plants over the last two centuries. PNAS 108:439–440

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Richardson DM, Thuiller W (2007) Home away from home—objective mapping of high-risk source areas for plant introductions. Divers Distrib 13:299–312

Ross LC, Lambdon PW, Hulme PE (2008) Disentangling the roles of climate, propagule pressure and land use on the current and potential elevational distribution of the invasive weed *Oxalis pes-caprae* L. on Crete. Perspect Plant Ecol Evol Syst 10:251–258

Siniscalco C, Barni E, Bacaro G (2011) Alien species distribution along the elevation gradient in the western Italian Alps. Plant Biosyst 145:150–158

Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob Change Biol 11:2234–2250

Trtikova M, Edwards PJ, Güsewell S (2010) No adaptation to altitude in the invasive plant *Erigeron annuus* in the Swiss Alps. Ecography 33:556–564

Walther GR, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I et al (2009) Alien species in a warmer world—risks and opportunities. Trends Ecol Evol 24:686–693

Williamson M (2006) Explaining and predicting the success of invading species at different stages of invasion. Biol Invasions 8:1561–1568

Willis SG, Hulme PE (2002) Does temperature limit the invasion of *Impatiens glandulifera* and *Heracleum mantegazzianum* in the UK? Funct Ecol 16:530–539

Woodward FI (1988) Temperature and the distribution of plant species. Symp Soc Exp Biol 42:59–75